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RESEARCH PAPER

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Human-induced globalization of insular herpetofaunas

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Abstract

Aim: The aim was to document the impact of the globalization of human activity on the biodiversity and biogeographical patterns of reptilian and amphibian faunas across islands worldwide.

Location: Islands worldwide.

Time period: From the 15th century to the present time.

Major taxa studied: Reptiles and amphibians.

Methods: We compiled lists of the reptilian and amphibian species that occurred on islands before the 15th century and of those that occur currently. For each species group, we calculated differences in species richness and in compositional similarities among islands, between the two periods. Regression models were used: (a) to associate the observed differences with spatial patterns of geographical, climatic, biotic and human factors; and (b) to quantify changes in the relative importance of non-human factors in explaining the spatial patterns of species richness and compositional similarity.

Results: The richness of reptile and amphibian species increased consistently across islands worldwide. Hotspots of increase were detected in the Caribbean and the Indian Ocean. The composition of species assemblages was substantially homogenized; this was particularly true for amphibians within the Caribbean Sea and for reptiles within the Caribbean Sea and Indian Ocean and between the Indian and the Pacific Oceans. Our results showed that spatial patterns of change in species richness and compositional similarity are driven by human and natural factors. The driving role of mean annual temperature is particularly consistent, and current reptile richness and compositional similarity patterns for both species groups are increasingly being shaped by the global temperature gradient.

Main conclusions: The globalization of human activity is eroding the regionalized character of insular herpetofaunas and leading to the emergence of global-scale gradients of taxonomic composition and species richness. Projections of increasing rates of biological invasions, extinctions and climate change suggest that these changes are likely to be aggravated even further in the coming decades.

KEYWORDS

amphibians, biogeographical regions, biotic homogenization, global biodiversity change, islands, reptiles, species richness

1 | INTRODUCTION

Human activities are changing the composition of species assemblages at unprecedented rates (Díaz et al., 2019; Dornelas et al., 2019). Insular biotas have been particularly affected, with many islands becoming hotspots of extinction and of establishment of alien species after human arrival and colonization (Dawson et al., 2017; Sax & Gaines, 2008; Spatz et al., 2017). Assessments of how these events are changing the taxonomic composition of insular biotas have focused primarily on changes to the species richness of each island and to the compositional similarity of species among the islands. These assessments highlight important deviations from natural biodiversity patterns and a strong taxonomic dependence on the magnitude of the changes caused. For example, although the richness of bird species across islands has remained relatively unchanged, owing to the number of established alien species that usually replace extinct ones, the insular plant species richness has increased dramatically (Sax, Gaines, & Brown, 2002). Likewise, the compositional similarity of taxa has generally increased, that is, insular biotas have become homogenized (Olden, Lockwood, & Parr, 2011); however, taxonomic groups can differ by nearly an order of magnitude increase (Longman, Rosenblad, & Sax, 2018). Despite the lack of cross-taxonomic generalities in the patterns of change in biodiversity on islands, thus far only the changes in a few taxonomic groups have been assessed comprehensively.

In this study, we assessed how human activity is changing the taxonomic diversity of reptiles and amphibians on islands worldwide and how these changes are reconfiguring their biogeographical patterns. To our knowledge, only a few studies have assessed the effect of human activities on the taxonomic diversity of insular herptiles in broad oceanic areas. In one of these studies, Ficetola and Padoa-Schioppa (2009) evaluated the long-term impact of human activities on reptile species richness in Mediterranean islands. In a similar study, Helmus, Mahler, and Losos (2014) focused on the effect of recent human activity on anole lizards in the Caribbean islands. Interestingly, the two studies obtained contrasting results for species richness. On the Mediterranean islands, the number of reptile species lost to human activity was not compensated by gains in alien species richness (Ficetola & Padoa-Schioppa, 2009). On the contrary, in the Caribbean, the number of anole species increased consistently across islands, owing to many introduced species becoming naturalized and the absence of species extinction events (Helmus et al., 2014). Notwithstanding these differences, both studies identified a strong imprint of human activity on the current geography of reptile richness.

In the present study, we focused on the taxonomic changes that have occurred since the onset of globalization. The focus on this period of human history, which has an ecologically significant start in the 15th century and extends until the present day (Crosby, 2003; Hulme, 2009), addresses both theoretical and practical considerations. First, it is during this period that human activity is likely to have caused the strongest changes in the diversity of herpetofauna on islands. This assumption is based on the combined effect of known factors, particularly many cases of first human contact with pristine islands. These led to a relevant number of extinction events, particularly for reptiles (Alroy, 2015; Case, Bolger, & Richman, 1992; Rhodin et al., 2015; Slavenko, Tallowin, Itescu, Raia, & Meiri, 2016), and a profusion of established alien species, many with wide, pan-oceanic invasion ranges (Capinha et al., 2017). Second, by restricting our analysis to the most recent centuries of human history, we are ensuring higher data completeness and reliability in terms of taxonomic changes (Case et al., 1992).

Beyond the expectation of substantial taxonomic changes, we hypothesized that the magnitude of these changes will have a predictable distribution. More specifically, it is likely that islands sharing similar colonial histories and human activity levels will have higher species compositional similarity, thereby reflecting commonalities in the species that were introduced or are extinct (Rhodin et al., 2015; Russell & Kueffer, 2019). Likewise, higher compositional similarity should be observed among islands with similar climates, thus highlighting the role of environmental filtering in the establishment of introduced species (Capinha, Essl, Seebens, Moser, & Pereira, 2015). The island characteristics that could drive changes in species richness are less clear. This is because changes in species richness result from a balance between species extinctions and the establishment of introduced species, two processes that often relate in opposing ways to human and ecogeographical factors (Dawson et al., 2017; Russell & Kueffer, 2019; Spatz et al., 2017). However, if one of these processes consistently prevails over the other, coherent geographical patterns are likely to emerge. If introduced species prevail over extinctions, increases in richness are likely to be greater where human activity has been more intense, thereby reflecting a greater number of introduced species (Dawson et al., 2017; Lockwood, Cassey, & Blackburn, 2009). The same is also true in areas where natural conditions favour the establishment of a diversified fauna, namely large islands with varied habitats (Ricklefs & Lovette, 1999) and (sub)tropical climates (Kier et al., 2009). Moreover, if extinctions prevail over introductions, the changes are likely to reflect mainly the intensity of human activity (Russell & Kueffer, 2019) and the size of the historical species pool, which mediates the number of extinctions that might occur.

To test these hypotheses, we compiled carefully curated lists of the extant reptiles and amphibians on islands at the onset of globalization (i.e., the historical baseline). We complemented this information by listing all the recorded extinction and introduced species establishment events that occurred until the present day. Based on these lists, we quantified the differences in species richness and compositional similarity between historical and current species assemblages. Then, we identified spatial hotspots of change and examined the roles of geography, the environment and human factors on the spatial distribution of species richness and compositional differences. Finally, we assessed how the historical and current species richness and compositional similarity patterns differ in their relationships with spatial patterns of geographical and environmental factors.

2 | METHODS

2.1 | Historical and current species assemblages

We used the scientific literature to compile lists of all known extant and extinct reptile and amphibian species in 64 island regions globally. We included both terrestrial and freshwater species, but excluded those dependent on marine resources, such as sea turtles and sea snakes. To increase the comparability of our results with those obtained for other taxonomic groups, our data search was directed mainly to island regions included in previous studies (e.g., Blackburn, Delean, Pyšek, & Cassey, 2016; Longman et al., 2018; Sax et al., 2002). However, other island regions for which we collected comprehensive information were also included in our study. The regions represented in our study were either single islands (e.g. Corsica) or island groups (e.g., São Tomé and Príncipe); however, each region was treated as a single unit in the analyses (hereinafter referred to as islands). The islands were distributed in the Atlantic (n = 19), Indian (n = 7), Pacific (n = 22) and Southern (n = 2) Oceans and in the Caribbean (n = 12) and Mediterranean Seas (n = 2). The delineation of oceanic regions followed "The World Factbook" (Central Intelligence Agency, 2008). A full list of the data sources used is provided in the Appendix. The locations of the island regions included in the study and the corresponding oceanic regions are shown in the Supporting Information (Appendix S1, Figure S1.1).

We aimed to compare the current species diversity with that having occurred before global oceanic exploration. To this end, we started by harmonizing the species lists according to the most recent taxonomic knowledge (for a schematic representation of the species data processing sequence, see Supporting Information Appendix S1, Figure S1.2). As much as possible, we used the taxonomic information provided by Frost (2019) and Uetz, Freed, and Hošek (2019) for amphibians and reptiles, respectively. A few species only recently identified were not included in these resources, and their original naming was retained. Based on the literature, we then classified each species on each island as native extant, native extinct or introduced; for the last of these categories, we considered only the species that became established (i.e., permanent additions to the insular faunas). Next, each species extinction and introduction event was classified according to its time of occurrence. Two temporal classes were considered: before and after the 15th century (< 1,400 and > 1,400 CE, respectively). Then, we assembled a baseline list for each taxonomic group and island that combined native extant species, extant species introduced before the 15th century and species that became extinct only during or after the 15th century (Supporting Information Appendix S1, Figure S1.2). One exception to this was the addition of the only record we found of a species that colonized by means of natural dispersal one of the island regions included in our study after 1,400 CE (*Iguana iguana* in Anguilla; Hodge, Powell, & Censky, 2011). This was a record of a species that is native to the island, and its inclusion in the baseline list allowed our analyses to focus exclusively on taxonomic changes caused by human activity.

Additionally, we compiled a second list (current assemblage) of all the native and introduced extant species (Supporting Information Appendix S1, Figure S1.2). The species inventories, with species status, timings of extinction or introduction and data sources used for each region are provided in the Supporting Information (Appendices S2 and S3).

2.2 | Island characteristics

We characterized the geography and environment of each island region and the human influence on each one using 13 variables. These variables were: (a) areal extent of the region (in square kilometres); (b) number of islands; (c) minimum distance to mainland (in kilometres); (d) origin of native biotas (coded as one for oceanic and zero if otherwise); (e) number of ecoregions; (f) mean annual temperature (in degrees Celsius); (g) mean annual precipitation (in millimetres); (h) current human population density (people per square kilometre); (i) absence or presence of human occupation before the arrival of Europeans (coded as zero or one, respectively); (j) the absence or presence of British colonization (coded as zero or one, respectively); (k) French colonization (coded as zero or one); (l) Portuguese colonization (coded as zero or one); and (m) Spanish colonization (coded as zero or one).

Data for the first three variables were collected by Weigelt, Jetz, and Kreft (2013). For regions composed of more than one island, the minimum distance to the mainland corresponded to the minimum value for the island group. The number of ecoregions was determined from the study by Olson et al. (2001). Mean annual temperature and mean annual precipitation data were collected from the study by Weigelt et al. (2013); for the multi-island regions, these variables corresponded to region-wide averages. Data for the remaining variables (i.e., origin of native biotas and those associated with human activity) were obtained from the studies by Blackburn et al. (2016), Longman et al. (2018), the United Nations Environment Programme (UNEP) Island database (http://islands.unep.ch) and Wikipedia (https://www.wikipedia.org/). Region-level values of each variable are provided in the Supporting Information (Appendix S4).

2.3 | Patterns and drivers of change in species richness

For each island and taxonomic group, we calculated the difference in the number of species between the historical and current species assemblages (hereafter, ΔSR). Negative values of ΔSR represented a reduction in total species richness, whereas positive values of ΔSR represented a gain in richness relative to the historical condition.

First, we investigated whether islands in distinct oceanic regions had significantly different Δ*SR* values. This analysis was performed using Mann–Whitney *U* pairwise tests, by comparing the Atlantic, Indian and Pacific Ocean and Caribbean Sea island values of Δ*SR*. Owing to low sample sizes, the Mediterranean Sea (n = 2) and Southern Ocean (n = 2) islands were not included in the comparisons.

Next, we tested for relationships between the island characteristics and the values of Δ*SR*. This analysis was performed using a generalized least squares (GLS) regression, a regression technique that considers the non-independence of observations that are geographically close (Dormann et al., 2007). In these models, Δ*SR* was associated with the aforementioned explanatory variables a–i (section 2.2) and one additional variable representing the species richness of the taxa in the historical assemblages (collected from the species lists; section 2.1).

The analyses of Δ*SR* did not inform us about the change in the relationship of species richness and the geography of non-anthropogenic factors. In order to evaluate this change, we used GLS regressions to compare the relationships of historical ($SR_{historical}$) and current species richness ($SR_{current}$) with spatial pattern variables describing the geography and environment of islands (variables a–g; section 2.2). We evaluated and compared the relationships of $SR_{historical}$ and $SR_{current}$ with each explanatory variable individually and for all variables combined.

To improve the robustness of the statistical significance of the GLS coefficients, we used logarithmic transforms of Δ*SR* and *SR* (Ives, 2015). The same transformation was applied to the following explanatory variables: number of islands, island area, human population density, distance from mainland and number of native species, in order to improve the linearity of their relationships with $\log_{10}$-transformed responses. To allow the transformation in the presence of negative values and zeros, we summed to Δ*SR* a constant corresponding to one plus the absolute positive of its minimum value. For the transformation of *SR* and the explanatory variables where a value of zero was present, a constant value of one was added in all instances.

We implemented GLS models that accounted for an exponential decay of spatial autocorrelation, given the highly regionalized character of island regions on a global scale (Dormann et al., 2007). Additionally, we tested for redundancies among the set of predictors using pairwise Pearson's correlations, *r*, and no variables were strongly correlated (r > |.7|) (Supporting Information Appendix S1, Figure S1.3). We also inspected for potential issues of multicollinearity among predictors by measuring the variance inflation factor (VIF) of each predictor, and none showed concerning multicollinearity levels (i.e., VIF > 10). The goodness-of-fit of GLS models was assessed by the pseudo-R^2 of Nakagawa, Johnson, and Schielzeth (2017).

The GLS models were implemented using the "nlme" package (Pinheiro, Bates, DebRoy, & Sarkar, 2016) of R v.3.5.1 (R Core Team, 2018). For the VIF calculations, we used the "vif" function of the "car" R package (Fox et al., 2012). Pseudo-R^2 was calculated with the "piecewiseSEM" R package (Lefcheck, 2016).

2.4 | Patterns and drivers of change in compositional similarity

We calculated the similarity in taxonomic composition between all pairs of islands, for the historical and current species assemblages. Calculations of compositional similarity corresponded to the inverse of Jaccard's dissimilarity, $CS = 1 - [(b + c)/ (a + b + c)]$, where a is the number of species occurring on both islands, b is the number of species found only on the first island and c is the number of species found only on the second island. This index returns values from one (indicating a fully similar taxonomic composition, i.e., all species are shared between the two islands) to zero (fully dissimilar composition, i.e., no species are shared). A total of 2,016 unique island pairs were compared. We also calculated the Δ*CS* between the current and the historical species assemblages for each island pair. Positive values of Δ*CS* indicated that the species compositions of the island pair grew similar owing to human influence, whereas negative values indicated that they became differentiated.

We used network-modelling techniques to visualize the grouping of islands based on the *CS* of the historical and current assemblages. In these visualizations, the study system was represented as a network, where each island was a node and the *CS* between the island pairs were represented as weighted links. This visualization was implemented using the "qgraph" R package (Epskamp, Cramer, Waldorp, Schmittmann, & Borsboom, 2012). In this tool, we used the Fruchterman–Reingold algorithm to estimate the two-dimensional layout of the network (Fruchterman & Reingold, 1991). This is an iterative algorithm representing the length of links as a function of their absolute weight. Accordingly, islands with higher levels of compositional similarity were grouped closer together, whereas those with lower similarity were shown further apart.

To complement the visual analyses of the spatial relationships represented by the networks, we quantified a few descriptive statistics of the compositional similarity values. These statistics were the average *CS* of the historical and current assemblages and the average Δ*CS* of islands within the same oceanic region and between islands belonging to different oceanic regions. The Mediterranean Sea and Southern Ocean were not included in these calculations, because only a single pair of islands represented each of these regions.

We also analysed whether Δ*CS* was associated with similarities in the geography, environment and human occupation of islands. For this purpose, we used multiple regression on distance matrices (MRM; Goslee & Urban, 2007). These models used the following explanatory variables: (a) geographical distance; (b) mean annual temperature; (c) total annual precipitation; (d) human population size; (e) the presence or absence (coded as one or zero,

respectively) of human occupation before European colonization; and the presence or absence (coded as one or zero, respectively) of (f) British; (g) French; (h) Spanish; and (i) Portuguese colonization. The geographical distances between the geographical centroids of islands were calculated by the great circle distance method using the "rdist.earth" function of the R package "fields" (Nychka, Furrer, Paige, & Sain, 2017). Pairwise differences of the remaining variables corresponded to Euclidean distances between the values of the two islands.

Finally, in order to evaluate the absolute effect of ΔCS on the naturalness of the spatial patterns of compositional similarity, we measured and compared the relationships of $CS_{historical}$ and $CS_{current}$ with the variables describing non-anthropogenic factors (variables a–c in the previous paragraph). The relationships were evaluated using MRMs, and each variable was considered separately and in combination with the others.

Multiple regression on distance matrices explicitly account for the non-independence of pairwise comparisons by performing tests of statistical significance of predictors based on permutations and a pseudo-*t* statistic (Legendre, Lapointe, & Casgrain, 1994). These models were implemented using the "ecodist" package in R (Goslee & Urban, 2007). A total of 9,999 permutations were used to assess the significance of coefficients.

3 | RESULTS

3.1 | Changes in species richness

From the 15th century to the present day, the establishment of introduced species was considerably more frequent than species extinctions were in both amphibians and reptiles (86 vs. 2 and 223 vs. 35, respectively). Across islands, both types of events were significantly more frequent for reptiles (average number of extinctions per island = 0.5 ± 1.17; average number of alien species per island = 3.5 ± 3.8) than for amphibians (0.03 ± 0.18 and 1.3 ± 1.7, respectively; $p < .05$; Mann–Whitney *U* pairwise test). Only two species were extinct on more than one island (*Crocodylus rhombifer* and *Mabuya mabouya*). About 38% of the introduced amphibian species (17 out of 45) and 42% of introduced reptile species (36 out of 86) colonized two or more islands. Of these, only six amphibian and 19 reptile species (accounting for 13 and 23% of the total number of species, respectively) were found in more than one oceanic region (Supporting Information Appendix S1, Table S1.1).

As a net result of the two types of events, many islands experienced gains in the total number of extant amphibian and reptile species (Figure 1a–d). The ΔSR values showed a left-skewed distribution, with most islands gaining up to four species (Figure 1b–d). Islands

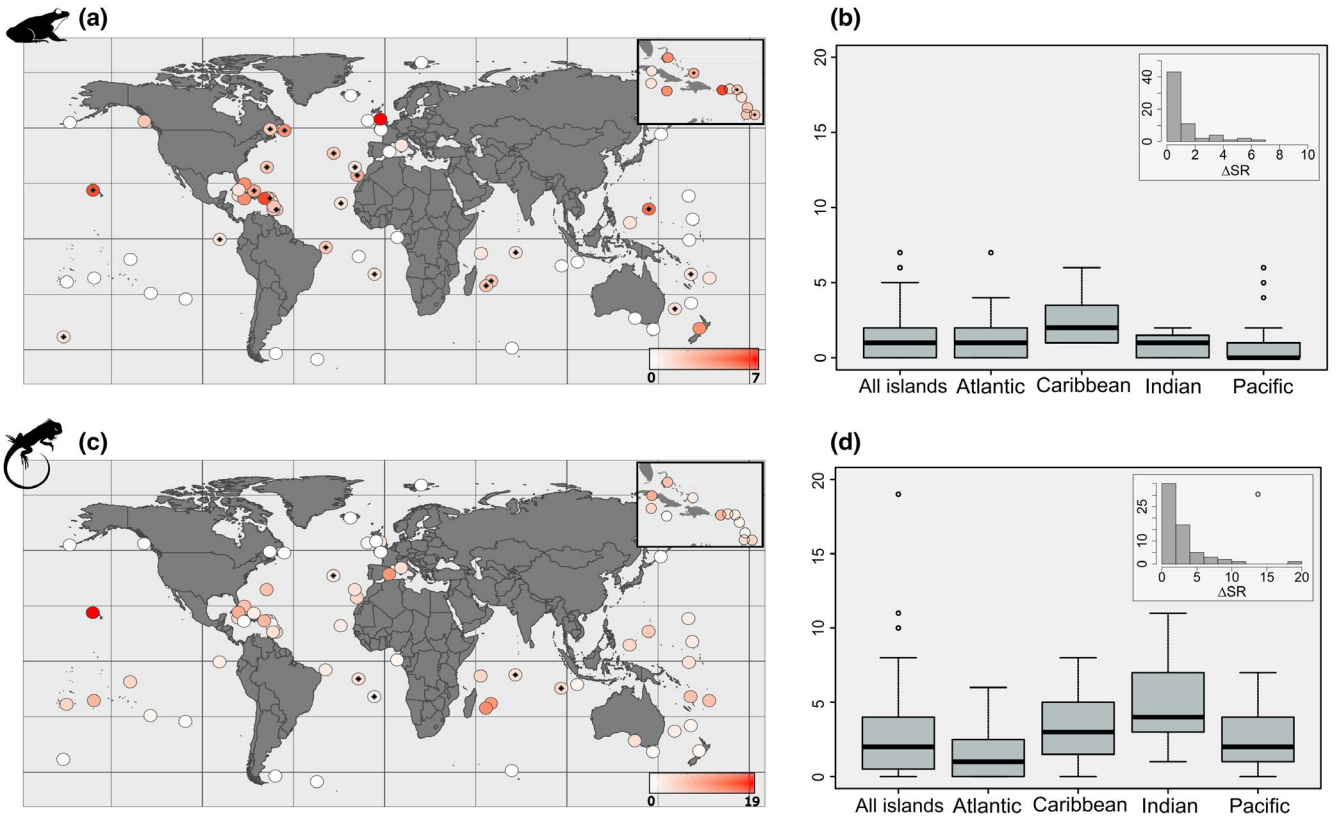

FIGURE 1 Difference between the number of (a,b) amphibian and (c,d) reptile species inhabiting islands at the onset of global oceanic exploration and the number of those species occurring there at present. (a,c) Inset maps depict the Caribbean Region in greater detail. The diamond symbol in maps identifies islands where all extant species were introduced after the 15th century. (b,d) Boxplots describe variation of differences in the number of species for all islands and for the four main oceanic regions represented in our data set. Inset histograms describe the number of islands per class of change in species richness

without amphibians were reduced by 54% (from 39 to 18; Figure 1a), whereas those without reptiles were reduced by 36% (from 14 to nine; Figure 1c). The percentages of change in species richness that were calculated for islands with species before the globalization of oceanic travel showed that the richness of amphibian and reptile species increased on average by 41 ± 53.2 and 48 ± 67.3%, respectively.

The results of the Mann–Whitney *U* pairwise tests for the Δ*SR* comparisons among oceanic regions confirmed that the gains in amphibian species richness were significantly higher on the Caribbean islands than in any of the other regions (Supporting Information Appendix S1, Table S1.2). The gains in reptile species richness of the Indian Ocean islands were significantly higher than those of the Atlantic Ocean islands, but not than those of the Caribbean or the Pacific islands (Supporting Information Appendix S1, Table S1.2). The gains in reptile richness of the Caribbean islands were significantly higher than those of the Atlantic Ocean islands.

Generalized least square models allowed the identification of variables consistently associated with the variation in Δ*SR* across islands. For amphibians, a pseudo-R^2 value of .52 indicated the ability of the model to explain a fair amount of variation in Δ*SR*. For this group, six variables were identified as having significant relationships (α = .05) with variations in Δ*SR* (Table 1). Areal extent, number

TABLE 1 Results of multivariate generalized least squared models explaining the $\log_{10}$-transformed difference between historical and current richness (Δ*SR*) of (a) amphibian and (b) reptile species across 64 island regions worldwide

Explanatory variable	Coefficient (*SE*)	*p*-value	Pseudo-R^2
(a) Amphibians			
Intercept	−1.1478 (0.439)	.012	.52
Geographical variables			
Area (log)	0.2013 (0.035)	**< .001**	
Number of islands (log)	−0.1361 (0.041)	**.002**	
Minimum distance to mainland (log)	−0.0576 (0.056)	.307	
Continental or oceanic	−0.3451 (0.189)	.074	
Environmental variables			
Number of ecoregions	0.1265 (0.050)	**.015**	
Mean annual precipitation	0.0001 (0.00008)	.142	
Mean annual temperature	0.0386 (0.012)	**.003**	
Biological variables			
Richness of amphibians in historical assemblages (log)	−0.3291 (0.086)	**< .001**	
Human-related variables			
Human population density (log)	0.0781 (0.0369)	**.039**	
Human occupation before Europeans	−0.1285 (0.137)	.354	
(b) Reptiles			
Intercept	−1.6625 (0.589)	.006	.58
Geographical variables			
Area (log)	0.1425 (0.050)	**.006**	
Number of islands (log)	0.0313 (0.053)	.558	
Minimum distance to mainland (log)	0.0469 (0.066)	.477	
Continental or oceanic	0.0424 (0.217)	.847	
Environmental variables			
Number of ecoregions	−0.0868 (0.058)	.143	
Mean annual precipitation	−0.0001 (0.0001)	.134	
Mean annual temperature	0.0707 (0.018)	**< .001**	
Biological variables			
Richness of reptiles in historical assemblages (log)	−0.0232 (0.100)	.818	
Human-related variables			
Human population density (log)	0.1030 (0.040)	**.014**	
Human occupation before Europeans	−0.0242 (0.162)	.882	

Note: Models used 10 explanatory variables representing four main types of putative drivers of the differences observed: Geographical, environmental, biological and human. Significant relationships are shown in bold ($p < .05$). Variation explained was measured by the pseudo-R^2 of Nakagawa et al., (2017).

of ecoregions, mean annual temperature and human population density were positively associated with gains in amphibian richness, whereas there was a negative association between the number of amphibians in historical assemblages and the number of islands. For reptiles, the variation in Δ*SR* explained by the model was slightly higher than it was for amphibians (pseudo-R^2 = .58; Table 1). Three variables were significantly (α = .05) associated with the Δ*SR* variation in reptiles: areal extent, mean annual temperature and human population density were all positively associated with Δ*SR* (Table 1).

The current relationships between the amphibian *SR* and the non-anthropogenic factor patterns deviated moderately from the corresponding relationships of pre-15th century species assemblages (Figure 2). The most relevant change in terms of individual variables concerned an increase in the explanatory power of areal extent (pseudo-R^2 increased from .16 to .26; Figure 2a). Taking into account all the geographical and environmental variables combined, the GLS models were able to explain a reasonably higher amount of variation in the current (pseudo-R^2 = .76) than in the historical amphibian *SR* (pseudo-R^2 = .63) (Figure 2f,g). These models also highlighted the importance of the role of geography over that of the environment as the main driver of amphibian *SR* patterns. In reptiles, the change in the relationship of geographical patterns of richness and non-human factors was more apparent and expressed mainly through a substantial increase in the explanatory power of mean annual temperature (pseudo-R^2 increased from .28 to .49; Figure 2i). Likewise, multivariate model analysis highlighted the importance of environmental factors over purely geographical factors as the main drivers of the distribution of reptile *SR* patterns (Figure 2l,m).

3.2 | Changes in compositional similarity

The average compositional similarity for the historical amphibian and reptile assemblages was very low (average pairwise $CS_{historical}$ = 0.002 ± 0.031 and 0.012 ± 0.066, respectively; Figure 3a,c). Most islands had no amphibian species in common (*n* = 48; 75%), except for a few islands in the Caribbean Sea and the north-eastern Atlantic. For reptiles, the number of islands without compositional relatedness was smaller (*n* = 21; *c*. 33%), and faunal regionalization was slightly more structured, because it involved a higher number of islands and the addition of a consistent cluster formed by Pacific islands.

The average compositional similarity of the current assemblages increased by *c*. 7.5 times for amphibians ($CS_{current}$ = 0.015 ± 0.069) and 2.1 times for reptiles ($CS_{current}$ = 0.025 ± 0.067). These increases led to substantial biogeographical reorganizations for both species groups. The compositional homogenization of amphibians was more accentuated among the Caribbean islands (Figure 3b; Supporting Information Appendix S1, Figure S1.4a), which now grouped tightly with a few islands from other regions, particularly the Pacific. The number of islands that had no amphibians in common was reduced almost by half, but still represented an important percentage of all islands (*n* = 25, *c*. 39%; Figure 3b). The compositional convergence of reptiles occurred mainly within the Indian Ocean, within the Caribbean Sea and between the Indian and the Pacific Ocean islands (Figure 3d; Supporting Information Appendix S1, Figure S1.4b). The number of islands that had no reptiles in common was reduced by more than half, thus representing a small percentage of the entire set of islands (*n* = 10, *c*. 16%).

The MRM results regarding Δ*CS* showed that longer geographical distances and larger differences in the average temperature between islands were negatively associated with increases of both amphibian and reptile compositional similarity (Table 2). Most importantly, these models explained only a very small fraction of the variation in Δ*CS* in both species groups (R^2 = .06 for amphibians and R^2 = .07 for reptiles).

The MRM results on the relationship between the historical and current *CS* patterns and the non-anthropogenic factor patterns showed that the globalization of human activity contributed to an increase in the explanatory power of geographical distances and of the mean annual temperature for both taxa (Figure 4). In both cases, the increase in mean annual temperature was higher than the increase in geographical distance. For amphibians, this caused a matching between the relative importance of environment and geography as predictors of current *CS* (Figure 4d), whereas for reptiles, environment is now the most important predictor (Figure 4h). Importantly, the amount of variation in current *CS* explained by the two types of factors remains small (R^2 = .08 for amphibians and R^2 = .18 for reptiles).

4 | DISCUSSION

4.1 | Patterns and drivers of change in species richness

Our results showed that, since the 15th century, there has been a considerable increase in both amphibian and reptile species richness on islands. Recent increases in insular species richness have been identified in vascular plants, mammals and freshwater fish (Blackburn, Cassey, Duncan, Evans, & Gaston, 2004; Sax & Gaines, 2008; Sax et al., 2002) but not in birds, a group whose species richness has remained relatively stable owing to the numbers of established alien species roughly matching those of extinct species (Sax et al., 2002). The consistently positive balance between herptile invasions and extinctions on islands is not surprising. First, islands appear to be particularly susceptible to the establishment of introduced species, including herptiles (Capinha et al., 2017; Dawson et al., 2017). The reasons behind this susceptibility remain an active topic of research, with factors commonly mentioned including a high diversity of introduced species (i.e., colonization pressure; Helmus et al., 2014; Lockwood et al., 2009), a low diversity of natural enemies and the naiveté of local prey (e.g., Jeschke, Debille, & Lortie, 2018; Moser et al., 2018). Second, the low or null diversity of native herptiles on many islands inherently limits the number of extinctions that can possibly occur. This limitation should be particularly

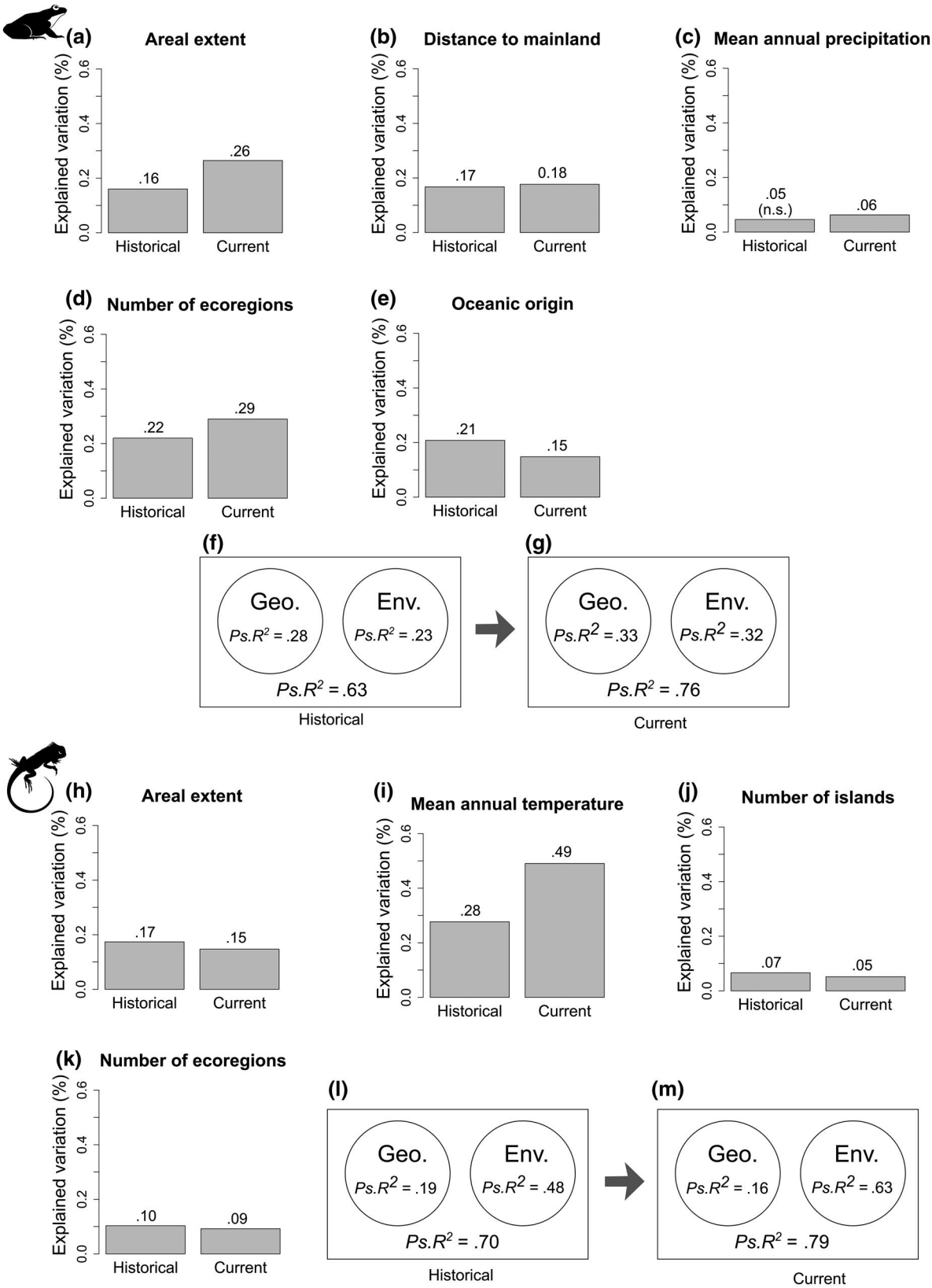

FIGURE 2 Proportion of variation in spatial patterns of richness of (a–g) amphibians and (h–m) reptiles explained by spatial patterns of geographical and environmental factors. Proportions are shown for species richness before the onset of global oceanic exploration ("historical") and for the present day ("current"). Measurements were made using generalized least squares models and considered each explanatory variable separately (bar plots) and all in combination (rectangles). For the latter models, the proportion of variation explained solely by geographical factors (Geo.) and by environmental factors (Env.) was also evaluated. Circles are not drawn to scale. Bar plots are shown only for individual variables having significant relationships ($\alpha = .05$). Reported values correspond to pseudo-R^2 ($Ps.R^2$)

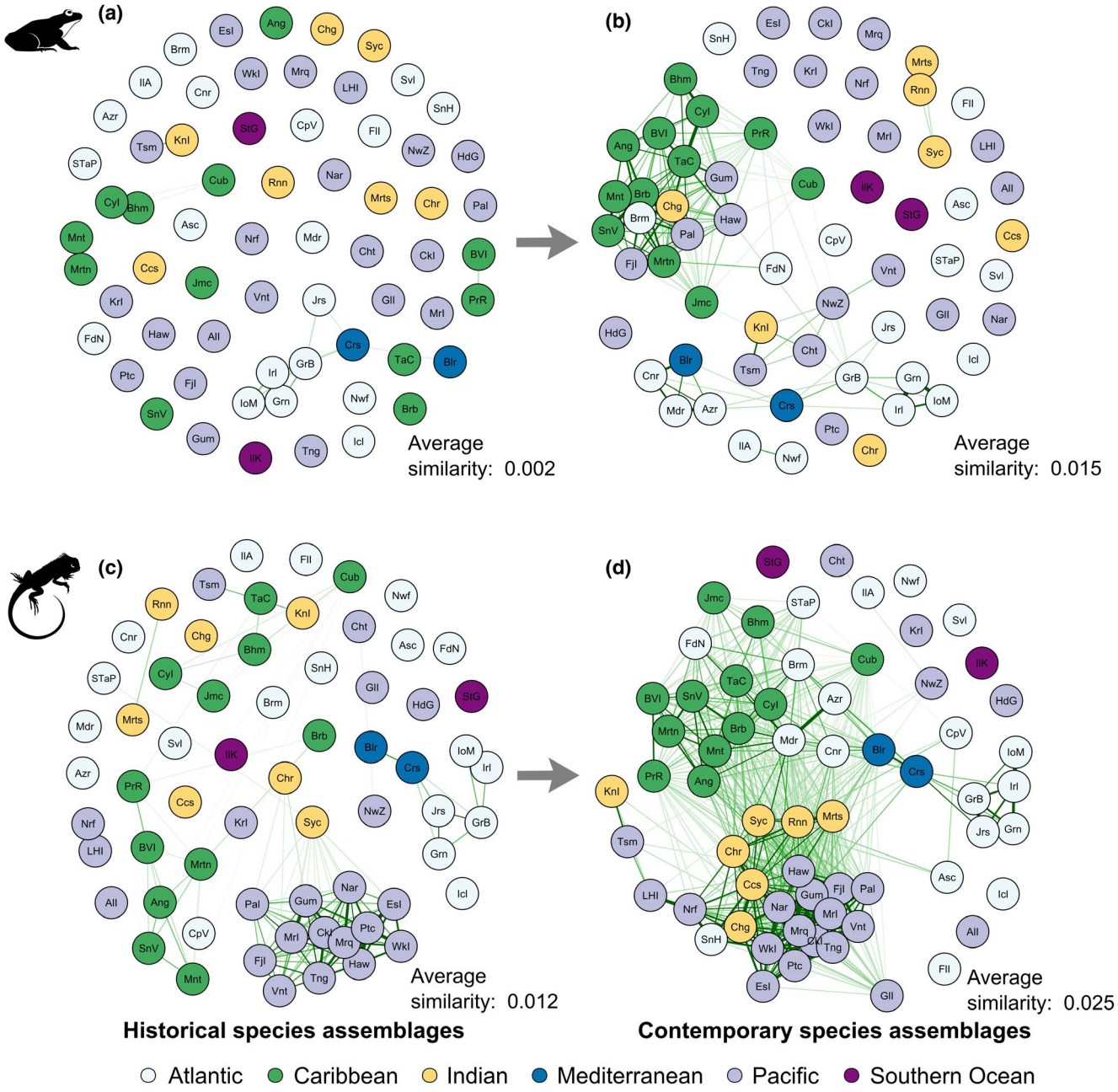

FIGURE 3 Clustering of islands based on levels of compositional similarity (as measured by the inverse of the Jaccard's dissimilarity index) for (a,b) amphibians and (c,d) reptiles. Clusters are shown for historical species assemblages, representing bioregionalization before the onset of global oceanic exploration and for current species assemblages. Islands are represented as nodes, and the compositional similarity between pairs of islands is represented as weighted links. The width and length of links is a function of compositional similarity, with thicker and shorter links representing higher similarity. Islands with higher compositional similarity are grouped closer together and those with lower compositional similarity are further apart. Names of regions and their abbreviatons are provided in the Supporting Information (Appendix S4).

relevant for both amphibians (e.g., *c*. 61% of the islands included in our study had no amphibians in the historical baseline) and reptiles (e.g., *c*. 22%). Finally, the diversity of herptile species targeted for direct exploitation by human explorers and settlers was apparently narrow. Direct human exploitation was a dominant cause of insular extinctions across taxa (Blackburn et al., 2004; Rhodin et al., 2015; Slavenko et al., 2016), and small-sized herptiles, which compose most of the taxonomic diversity on islands, have remained largely free from these pressures (Rhodin et al., 2015; Slavenko et al., 2016), substantially reducing their chances of becoming extinct.

Given the prevalence of invasions over extinctions, the results of the regression models associating spatial variables with variations in change in richness are consistent with our expectations. Both species groups showed higher gains in richness on islands where the human population density, areal extent and mean annual temperatures were higher. Human population density is a proxy for

TABLE 2 Results of multivariate regression on distance matrices (MRMs) explaining difference between historical and current compositional similarity of assemblages (ΔCS) of (a) amphibians and (b) reptiles

Explanatory variable	Coefficient	*p*-value	R^2
(a) Amphibians			
Intercept	0.04933	< .001	.06
Geographical variable			
Geographical distance	< −0.000002	**< .001**	
Environmental variables			
Mean annual temperature	−0.00148	**< .001**	
Mean annual precipitation	0.000003	.414	
Human-related variables			
Human population size	< −0.000001	.155	
British colonization	−0.00565	.069	
French colonization	0.00216	.606	
Portuguese colonization	−0.01148	.255	
Spanish colonization	−0.00122	.849	
Human occupation before Europeans	−0.00164	.641	
(b) Reptiles			
Intercept	0.03262	< .001	.07
Geographical variable			
Geographical distance	−0.000001	**< .001**	
Environmental variables			
Mean annual temperature	−0.00130	**< .001**	
Mean annual precipitation	< 0.00001	.685	
Human-related variables			
Human population size	< −0.00001	.462	
British occupation	0.00038	.864	
French colonization	0.00308	.291	
Portuguese colonization	−0.00814	.221	
Spanish colonization	−0.00261	.553	
Human occupation before Europeans	0.00508	.073	

Note: Historical and current compositional similarities were calculated between each pair of islands, for 64 islands dispersed worldwide. The models used nine explanatory variables, representing geographical, environmental and human relatedness among islands. Significant relationships are shown in bold ($p < .05$), based on 9,999 permutation tests.

the volume of goods that are imported and the amount of human travel to and from islands, and thus plays a driving role in the number of species introduced (e.g., via pet trade and as stowaways in cargo) (Dawson et al., 2017). The relationships identified for the areal extent agree with the expectations for higher diversity in wider areas (MacArthur & Wilson, 2001). The relationship identified for the annual mean temperature also makes ecological sense, because it is likely to express the inability of most herptiles to withstand cold climates (Storey, 1990). Amphibians had a significant, positive relationship with the number of ecoregions and negative relationships with historical species richness and the number of islands. The former relationship is supportive of a positive, often identified, effect of habitat diversity (Ricklefs & Lovette, 1999). The relationship with historical species richness could suggest a role for the biotic resistance of the pre-exiting community over introduced species (Jeschke et al., 2018). The possibility of this relationship resulting from higher potential for extinctions on islands with larger historical species pools might seem more parsimonious, but only two amphibian extinction events were recorded. The negative relationship with the number of islands is unclear and, possibly, corresponds to an offsetting of the areal extent effect when wide areas were obtained from the combination of a high number of islands.

The loss of naturalness in the spatial patterns of species richness was substantial for both species groups. Interestingly, human action caused an increase and not a decrease in the predictability of patterns of richness from patterns of geographical and environmental factors. In amphibians, the increase in predictability was driven mostly by the areal extent and the number of ecoregions; wide islands with higher habitat diversity currently host a consistently higher number of amphibian species than they did before globalization. Moreover, the explanatory power of the distinction between oceanic and non-oceanic islands, which is commonly used to differentiate between species-poor and species-rich islands (e.g., Longman et al., 2018), was reduced. In reptiles, the higher predictability of current patterns of species richness distribution was driven primarily by a strong increase in the role of mean temperature. The strong increase in the role of this variable was also apparent in the map of changes in richness (Figure 1c), where the highest gains in richness were observed mainly on islands at lower latitudes. This pattern is likely to express, to some extent, the inability of introduced species to become established successfully on higher latitude islands characterized by cold climates (Storey, 1990).

4.2 | Patterns and drivers of change in compositional similarities

There were substantial increases in the average compositional similarity of both reptilian and amphibian species. The current average compositional similarity of reptiles was more than two times higher than it was before the 15th century; in amphibians, this value was almost eight times higher. These values are higher or on par with the increases recorded for vascular plants and birds after the first human occupation of oceanic islands (Rosenblad & Sax, 2017), but are lower than those recorded for mammals on islands worldwide (Longman et al., 2018). The much higher relative increase of amphibian compositional similarity is likely to be a result of the very low levels of initial (historical) similarity, which amplify the homogenizing effects of same-species introductions between islands, as was also verified for mammals (Longman et al., 2018).

The increases in compositional similarity that were observed caused a marked reshaping of the bioregionalization of islands on a global scale. This reshaping was dominated by the biotic convergence

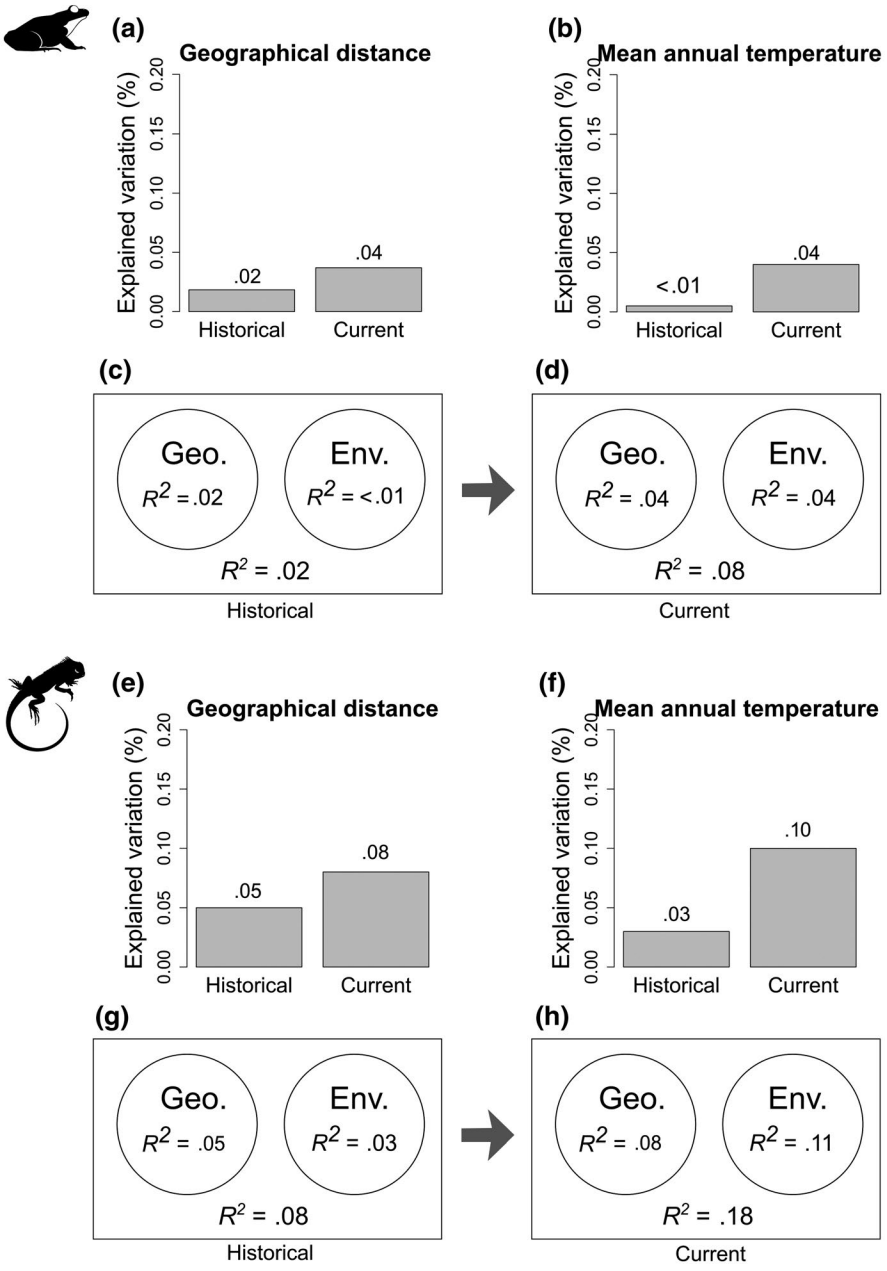

FIGURE 4 Proportion of the variation in spatial patterns of compositional similarity for (a–d) amphibians and (e–h) reptiles, explained by patterns of geographical proximity and of environmental similarity between islands. The amount of variation explained (R^2) was quantified using multiple regression on distance matrices, and measurements were made for historical species assemblages ("historical") and for the current assemblages ("current"). Regression models considered each explanatory variable separately (bar plots) and all in combination (rectangles). For the latter models, the proportion of variation explained by geographical factors (Geo.) and by environmental factors (Env.) is also shown. Circles are not drawn to scale. Bar plots are shown only for variables with significant relationships (α = .05)

of islands within the Caribbean (for both species groups) and within the Indian Ocean (for reptiles), but also between many islands located in distinct oceanic regions (e.g., in the Indian and the Pacific Oceans for reptiles). The results of the regression analyses show that island pairs that were close to each other had significantly higher increases in compositional similarity, which is likely to reflect a degree of spatial regionalization in the distribution of human-mediated events of invasion and extinction. However, compositional similarities are now equally or better explained by thermal similarities than by geographical distances as opposed to what was true before the onset of globalization. Temperature plays a part in environmental filtering, with thermal conditions acting in favour of certain introduced species. This finding is consistent with the hypothesis of an increased correspondence of global biogeographical regions to global climatic patterns driven by biological invasions (Capinha et al., 2015). It should, however, be noted that the models could explain only a modest fraction of variation in the compositional differences of the two species groups. The explanatory variables used in these models reflect general patterns of geographical, environmental and human-related similarities between islands, and their limited explanatory power suggests a high importance of episodic, eventually idiosyncratic, drivers of alien species establishment and of species extinction. This is unsurprising given the large number of distinct human disturbances and complex global trade and travel flows that mediated the types and magnitudes of species extinctions and introductions on islands over the last centuries (Russell & Kueffer, 2019). In our models, we tested for evidence that British, French, Portuguese and Spanish colonial empires helped to reshape insular biodiversity. Future work could elucidate the role of human influence further by representing more accurately the flows of people

and goods between islands and between islands and continental areas throughout the years. However, we anticipate that the lack of detailed data on these flows for most islands would be a difficult obstacle to overcome.

4.3 | Conclusion

Our work provided the first global-scale assessment of how the diversity and biogeography of insular herpetofaunas have changed since the onset of globalization. We found widespread increases in species richness and substantial faunal homogenization. Somewhat paradoxically, human activity has introduced an increasing agreement between the spatial patterns of herptile richness and compositional similarity and the spatial patterns of some non-human factors, particularly the global temperature gradient. This increasing agreement appears to be driven primarily by biological invasions and reflects a reduction in the role of natural dispersal barriers, allowed by human agency, and an increase in the role of ecological factors in determining the number and identity of species colonizing islands. Altogether, our findings substantiate the growing body of literature identifying anthropogenic activities as a major agent of biodiversity and biogeographical alteration on a global scale (Capinha et al., 2015; Díaz et al., 2019; Dornelas et al., 2019). Recent projections of high rates of herptile species invasions and extinctions (Alroy, 2015; Seebens et al., 2017), combined with fast-changing climatic patterns (Foufopoulos, Kilpatrick, & Ives, 2011; Stocker, 2014), suggest that insular herpetofaunas are likely to undergo further substantial changes in the coming decades.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

C.C. designed the study with contributions from L.R.; C.C. and F.M. compiled and prepared the data; C.C performed the data analysis; C.C. led manuscript writing, with input from F.M. and L.R.

DATA AVAILABILITY STATEMENT

All data necessary to reproduce the analyses presented in this study are included in the Supporting Information (Appendices S2–S4).

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BIOSKETCH

César Capinha is a biogeographer with interests in biological invasions, global biodiversity change and predictive modelling.

Fabio Marcolin is an ecologist and ornithologist interested mainly in conservation ecology and wildlife management. Recently, he became interested in understanding how conservation strategies should be implemented to mitigate ecological problems arising from biological invasions.

Luís Reino is an ecologist and ornithologist interested in a broad range of topics, including biological invasions. In invasion ecology, L.R. is particularly interested in documenting how global change is shaping the spatial patterns of human-mediated dispersal of species.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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APPENDIX 1

DATA SOURCES

Abrahão, C. R., Russell, J. C., Silva, J. C. R., Ferreira, F., & Dias, R. A. (2019). Population assessment of a novel island invasive: tegu (*Salvator merianae*) of Fernando de Noronha. In: C. R. Veitch, M. N. Clout, A. R. Martin, J. C. Russell & C. J. West (Eds.), *Island invasives: scaling up to meet the challenge*, (Vol. *62*, pp. 317–325). Occasional Paper SSC no. 62. Gland, Switzerland: IUCN.

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